The Researches of Bouvier and Bordage on Mutations in Crustacea of the Family Atyidæ.

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With 4 Text-figures.

Some six years ago Professor E. L. Bouvier ('04, '05)[1] called attention to the remarkable dimorphism of certain tropical river-prawns of the family Atyidæ, which he compared with the phenomenon of mutation described by de Vries in the vegetable kingdom. He pointed out that the case was especially noteworthy, not only because of the marked discontinuity and constant occurrence of the variations, but also because they affected characters regarded as distinctive of genera; and he drew the conclusion that these genera had originated by a process of mutation. M. E. Bordage has recently published ('08, '09A, '09B) the results of some observations and experiments on the living animals which seem to support Bouvier's views, and to indicate, at all events, a promising field for further investigations. At the suggestion of Sir Ray Lankester the following account has been prepared in the hope that it may induce some naturalists, who have the opportunity of studying the animals under natural conditions, to give attention to the matter.

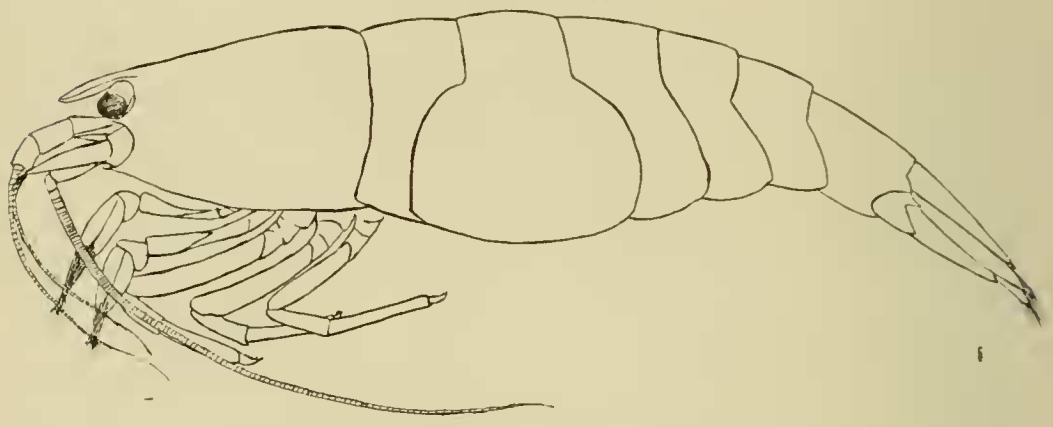
The Atyidæ (see Text-fig. 1) are a family of Decapod Crustacea belonging to the tribe Caridea (which includes most of our common prawns and shrimps), and are widely distributed in fresh waters in the warmer regions of the globe (see Ortmann

[1] The numbers refer to the list of papers on p. 796.

'94, and Bouvier '05). Some of the members of the family show very primitive characters, having, for instance, swimming branches or exopodites on all the thoracic limbs, as in the so-called "Schizopods." In this and in other features they resemble the deep-sea Hoplophoridæ, from which, or from some allied forms, most authorities are agreed in considering them to have been derived.

Other members of the family, however, are considerably specialised. In some characters this specialisation has proceeded along lines parallel to those followed in other series of the Caridea—for example, in the progressive disappearance

TEXT-FIG. 1.



Atya bisulcata. Ovigerous female of the Atya-form. × 3. From a specimen in the "Challenger" collection from Honolulu.

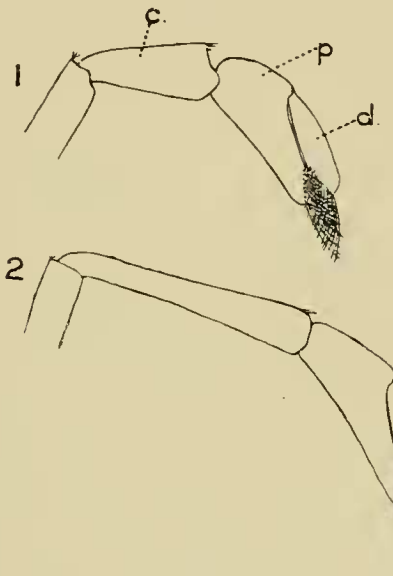
of the exopodites and, later, of the epipodites of the legs, and a diminution in the number of the branchiæ. In other characters specialisation has followed lines peculiar to the family, and this is especially the case with the modifications of the chelate first and second pairs of legs. In nearly all Atyidæ these limbs are comparatively small, not dissimilar in size, and have the fingers each tipped with a brush of long hairs (Text-fig. 1). Fritz Müller ('92) has described how these brushes are used in collecting pellets of mud on which the animal feeds.[1] Among the more specialised members of the

[1] I do not understand Bordage's statement that the chelæ are used for excavating burrows in the mud, for which their structure would appear to be ill-adapted.

family the characters used as distinctive of the genera are chiefly drawn from the modifications of the chelipeds, and some of these may now be considered in fuller detail.

In the very numerous species of the genus Caridina (Text-fig. 2) the chelæ themselves do not differ greatly, except in carrying brushes of setæ, from the typical form found in many other Decapods. The dactylus (*d.*) or terminal segment of the limb, forming the "movable finger," is opposed to a thumb-like process ("immovable finger") of the penultimate

TEXT-FIG. 2.



Caridina nilotica var. 1, 2, first and second chelipeds. *c.*, carpus; *d.*, dactylus; *p.*, palmar portion of propodus. × 40. From a specimen collected by Dr. W. A. Cunnington in the Victoria Nyanza.

segment or propodus. The proximal part of the propodus, expanded to contain the muscles moving the dactylus, forms what is known as the "palm" (*p.*) of the chela. In Caridina the two pairs of chelipeds differ in the form of the segment which supports the propodus, the "wrist" or carpus (*c.*). In the second pair it is more or less elongated and slender, and the propodus articulates with its distal end; in the first pair, on the other hand, it is short and broad, its distal margin is more or less concave (cf. Text-fig. 2, 1, and Text-fig. 4, *A'*), and the propodus articulates with its lower corner.

The species of the genus Ortmannia (formerly known as Atyoida) differ from those of Caridina chiefly in the fact that the carpus of the second pair resembles that of the first pair (Text-fig. 3, *B'*, *B''*), being short and broad, with its distal margin excavated and articulating with the propodus at its lower corner. It is to be noted that these characters are not equally well marked in all the species referred to Ortmannia; in some the second carpus is still, as in Caridina, somewhat longer than the first, and the excavation of its distal margin is shallow (as in Text-fig. 4, *B''*); in other species the carpus is nearly similar in the two pairs and so deeply excavated as to assume an almost crescentic form (as in Text-fig. 3, *B'*, *B''*). Associated with this excavation of the carpus is a shifting (already begun in Caridina) of the carpo-propodal articulation from the proximal end to the lower border of the propodus. Further, while in some species the chelæ themselves are quite similar to those of Caridina, in others the "palm" is much shortened, or, in other words, the articulation of the movable finger is carried backwards towards the base of the propodus.

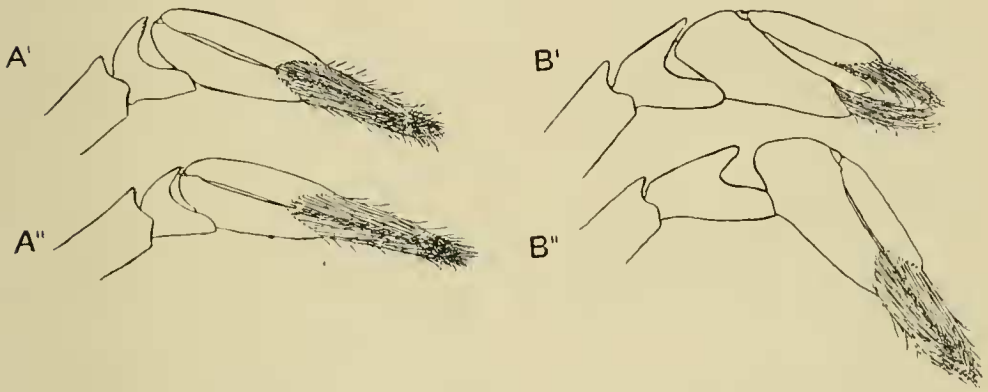
These modifications lead towards the conditions found in the genus Atya, which includes the largest and most highly specialised members of the family. In these the two pairs of chelipeds (Text-fig. 3, *A'*, *A''*) are quite similar, and the carpus is reduced by the excavation of its distal border to a narrow crescent, with the lower limb of which the propodus articulates. The propodus itself assumes a form unlike that of any other Decapod; the backward shifting of the articulation of the dactylus has been carried so far that the palm has entirely disappeared, and the chela is composed of two similar parts, hinged together at one end, like the legs of a pair of compasses.

Although, within each of the genera, there is some variation in the degree to which these characters are developed, this variation is so far discontinuous that all the known species could, prior to Bouvier's researches, be referred without much difficulty to one or other of the genera. If it be objected that such apparently trivial differences should

not be regarded as of generic value, it may be pointed out that, as a rule, though not in every case, they are coincident with other features which help to characterise, although they do not define, the generic groups; and further, there is no criterion by which the generic value of a character may be estimated, except that of its constancy throughout a group of species.

Bouvier's discovery may be shortly expressed by saying that certain species were found to be dimorphic and to oscillate, as it were, in a state of unstable equilibrium between one generic group and the next. Thus, Miss Rathbun ('01)

TEXT-FIG. 3.



Atya bisulcata. *A'*, *A''*, First and second chelipeds of the Atya-form. *B'*, *B''*, First and second chelipeds of the Ortmannia-form (Ortmannia Henshawi). × 7. From specimens in the "Challenger" collection from Honolulu.

had described a new species, Ortmannia Henshawi (Text-fig. 3, *B'*, *B''*), found in association with Atya bisulcata (*A'*, *A''*), on the island of Hawaii; Bouvier pointed out that this association was not accidental, but constant, that the two forms were indistinguishable, except by the characters of the chelipeds, and that they should be regarded as constituting a single dimorphic species. He found a similar phenomenon in the case of Atya serrata, described by Spence Bate from specimens obtained by the "Challenger" Expedition at the Cape Verde Islands, and since found in many localities on the islands of the Indian and Pacific Oceans. To the Ortmannia-form of this species Bouvier gave the name

O. Alluaudi. In both species the two forms were sharply distinguished, although in the Ortmannia individuals (especially in O. Alluaudi) a considerable amount of variation was observed in the relative proportions of the fingers and palm of the chelæ; the Atya-form, on the other hand, presented no noteworthy variation. In both species Bouvier found that the dimorphism was independent of age and sex; both forms were found through a wide range of size, although the Atya individuals were, on the whole, somewhat larger, and females of both were observed carrying eggs. In the case of A. bisulcata (O. Henshawi) both forms occurred in about equal numbers; in A. serrata (O. Alluaudi) there was some evidence that the relative proportions varied in different localities.[1]

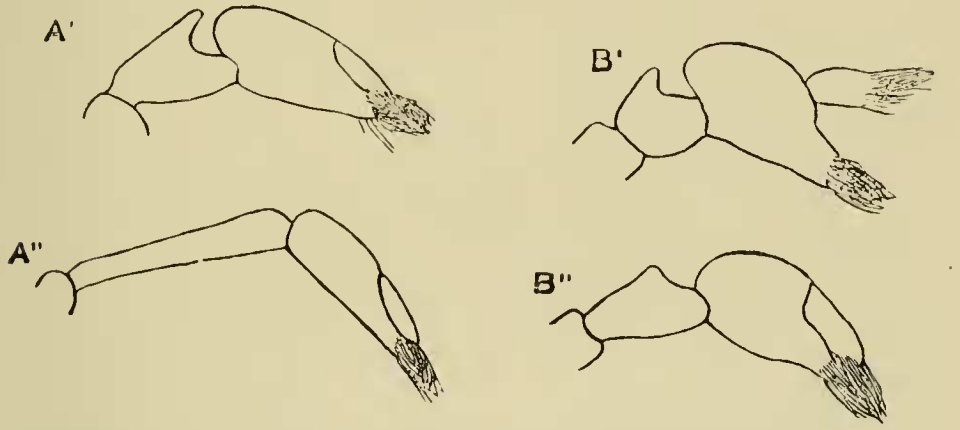
In one species of Caridina Bouvier found evidence of the existence of an analogous mutation leading to the genus Ortmannia. Among eleven examples of C. apiocheles (Text-fig. 4) (probably from the Seychelles), he observed one in which the carpus of the second pair of chelipeds (Text-fig. 4, *B″*), instead of being long and slender as in the typical individuals, was short, broad, and excavated distally, resembling that of the first pair, so that the specimen, had it occurred alone, would have been referred to Ortmannia. In this case, however, it remains to be seen whether the

[1] It may be of interest to give here the results of a preliminary examination of the material of these two species in the British Museum collection. In one lot of Atya bisulcata obtained by the 'Challenger' Expedition at Honolulu forty-two specimens are of the Atya-type and forty-six of the Ortmannia-type. Only one specimen cannot be referred to either, having three chelæ of the Atya-shape, while the fourth is distinctly of the Ortmannia-shape. There is a considerable amount of variation in the chelæ of the Ortmannia-individuals, and their terminal brushes of setæ are always much shorter than in the Atya-individuals. In a second lot of specimens from Hawaii only nine Ortmannia-individuals are found among thirty-eight Atya-individuals. Of the two type-specimens of Atya serrata from the Cape Verde Islands in the 'Challenger' collection, the larger is of the Atya-type while the smaller is a distinct Ortmannia.

occurrence of the mutation is a normal and constant feature of the species.[1]

Professor Bouvier discusses at length the possible explanations of these curious phenomena. He points out that it is impossible to continue to regard Atya bisulcata and Ortmannia Henshawi, for instance, as distinct and independent species; their constant association and their identity in all characters except those of the chelipeds forbid their separation, and it may be added that Professor Bouvier's proved skill and experience as a carcinologist give special weight to his opinion on this point. He also dismisses, and no doubt

Text-fig. 4.



Caridina apiocheles. *A'*, *A"*, First and second chelipeds of the typical Caridina-form. *B'*, *B"*, First and second chelipeds of the Ortmannia-form (O. Edwardsi). After Bouvier.

rightly, the suggestion that the phenomena are due to hybridisation; and he concludes that the facts he describes have their closest analogy in the "mutations" of de Vries.

[1] The question whether the genera implicated in these phenomena of mutation are to be retained as valid is of secondary importance, and hardly concerns more than the convenience of the systematist. If they are to be retained, however, it would seem that a good case exists for the re-instatement of the name Atyoida in place of Ortmannia. Miss Rathbun displaced Atyoida on the ground that the surviving type-specimens of Randall's Atyoida bisulcata, the type-species of Atyoida, have chelæ of the Atya-type. If, however, O. Henshawi, the type-species of Ortmannia, is only a form of A. bisulcata, the two genera are synonymous and the older name should be used.

Instead of being limited to comparatively trivial characters and giving rise to varieties or "petites espèces" as in de Vries's examples, the mutations of the Atyidæ affect characters of generic importance. Bouvier believes that the course of evolution from the more primitive Caridina to the specialised Atya has been discontinuous, proceeding at a single step from Caridina to Ortmannia and again from Ortmannia to Atya, and that the species mentioned remain in the condition of instability accompanying the transition from one to the other. It is also implied, although Bouvier does not dwell on the point, that these genera are polyphyletic and have originated independently in several regions of the globe.

There is still another possibility, not alluded to by Bouvier, that deserves mention here, namely, that the apparent dimorphism is due to heteromorphic regeneration of the chelipeds after mutilation. Many cases are now known among Arthropoda in which regenerated appendages depart from the normal type, and not infrequently revert to a simpler and more primitive form ("régénération hypotypique" of Giard). Although the chelipeds of many Atyidæ readily break off from the body in preserved specimens, it seems very improbable that this mutilation should happen so frequently in nature that 50 per cent. of the specimens collected would have regenerated limbs; nor is it less improbable that all four chelipeds would be removed simultaneously[1]; and the experiments of Bordage, described below, lend no support to this suggestion.

Professor Bouvier pointed out the desirability of testing his conclusions by observation and experiment on the living animals, and it was at his suggestion that Bordage undertook the researches of which the results are presented in his recent papers ('08, '09A, '09B). On the island of Réunion Ortmannia alluaudi, with its mutation Atya serrata, occurs abundantly in mountain streams at altitudes above 300 mètres. Owing to the high temperature prevailing at the

[1] Only one case has been noticed in which one of the chelipeds differed from the others (see above, p. 790, footnote).

coast (St. Denis), where the experiments were carried on, it was impossible to keep the animals alive in small aquaria, but after several failures Bordage succeeded in keeping living specimens in a small tank of masonry through which a current of water from the town supply was kept flowing. The inflow and outflow were guarded by fine wire gauze covered with muslin to prevent the escape of adults or larvæ, or the accidental introduction of additional specimens. A single ovigerous female of the Ortmannia form was placed in the tank, and in a few days numerous zoea larvæ were observed in the water. Only seven individuals survived to assume the perfect form a fortnight later, and these proved to be all, like the parent, of the Ortmannia-type. A second experiment, however, was more successful. Another ovigerous Ortmannia was placed in the tank (which had been emptied and cleaned out between the experiments) and the larvæ were hatched in due course. When they were about to pass into the final stage of their metamorphosis some weeks of torrential rain rendered the water-supply muddy and opaque, so that the young prawns were lost sight of. On cleaning out the tank, however, sixteen specimens were discovered among the mud, and of these ten were like the parent, while six were of the Atya-type. Bordage assures us that the precautions he took absolutely exclude the possibility of these young prawns having come from any source other than the eggs carried by the original female. In another experiment two females of the Atya-type produced twenty-seven young, all of which resembled the parents. Bordage states that he was unable to obtain fecundation of Ortmannia females by Atya males, while they bred readily with males of their own type.

These results are somewhat surprising, and can hardly be accepted as final without a good deal more experimental evidence. If the two forms do not interbreed, and if, as Bordage considers probable, the Atya-form always breeds true, it is evident that the Ortmannia-form would disappear (in the absence of a selective death-rate operating in its

favour) even more speedily than is required by the "loi de Delboeuf" to which Bouvier refers.

Bordage also made some experiments on the regeneration of the chelipeds. He found that after amputation of the chelipeds of an Atya, the regenerating limbs had at first the Ortmannia-form—that is to say, the propodus showed a distinct palmar portion. At the first moult after the operation, however, the Atya-form was assumed, the articulation of the dactylus having shifted to the proximal end of the propodus. It is not clear from the account given whether the chelæ were perfectly formed and movable before the first moult. Bordage regards this as a typical case of atavistic regeneration (régénération hypotypique), and he also cites a case described by Fritz Müller ('92) as showing that the regenerated second pair of chelipeds in Ortmannia potimirim have an elongated and slender carpus like that of Caridina.[1]

While Bordage's results are highly interesting and suggestive, they rest upon a very narrow basis of experimental evidence. There seems to be no reason to doubt his statement that young of the Atya-type were hatched from the eggs of an Ortmannia female, but it is based on the result of a single experiment carried out under unfavourable conditions, and no figures of the young prawns are given. The supposed inability of the Atya females to produce Ortmannia young rests also on the negative result of a single experiment and the simple statement that the two forms do not interbreed deserves to be examined in greater detail. It would be of interest to have further particulars as to the normal course of development in the two forms, and to know whether there is any trace of an Ortmannia stage in the development of the Atya-form of cheliped. The phenomena of regeneration also require more thorough investigation; it is possible that, as is

[1] It may be mentioned that a comparison of Müller's original figure with the copy given in Bordage's paper does not increase our confidence in the diagrammatic drawings which the latter author gives to illustrate his own observations.

known to be the case in other Decapods, the form of the regenerated limbs may differ according to the age of the individuals experimented on. While it is very improbable, for the reasons stated above, that the whole appearance of dimorphism can be due to regeneration, it remains to be tested whether the form of the chelipeds does really remain constant throughout the life of the individual. Apart from the possibilty of further experiments with the living animals, it would be of importance to get together sufficient material for a biometrical investigation into the degree of discontinuity in the variation and its incidence in relation to age, sex, and locality.

One of the most interesting features of these mutations, if Bouvier's interpretation of them be confirmed, is the direct way in which they bear on the problems suggested by a study of the Atyidæ from the systematic standpoint. This may be illustrated by an example. In Lake Tanganyika (Calman, '99 and '06) the collections of Mr. J. E. S. Moore, and, more especially, of Dr. W. A. Cunnington, have revealed the existence of numerous peculiar species of Atyidæ, which differ from all the other members of the family (with one exception to be mentioned presently) in having a reduced branchial formula. Thus the Tanganyikan Caridella resembles Caridina in most of its characters, except that it has no pleurobranchia on the last somite of the thorax, and Atyella differs in the same character from Ortmannia. I have pointed out elsewhere that while the reduction in the number of branchiæ may have occurred independently in each of the Tanganyikan genera, so that Caridella may be supposed to be derived from Caridina, and Atyella from Ortmannia, Bouvier's results suggest as a possible alternative that Atyella may have originated from Caridella by a mutation parallel to that by which, in other parts of the world, Caridina has given rise to Ortmannia. The latter hypothesis has recently received the support of Prof. Bouvier himself ('09A, '09B), in connection with his very interesting discovery that Atya Poeyi

of the West Indian Islands has the same branchial formula as Caridella and Atyella, and in fact only differs from the last-named genus in having chelæ of a distinctly Atya type. He refers the West Indian species to a new genus, to which he gives the name Calmania. He supposes it to have been derived from Atyella in the same way as Atya from Ortmannia, and he concludes that Atyella (and Caridella also) must formerly have existed in America. From this view I would venture to dissent. Even if the phenomena of mutation lead us to believe that similar forms of chelipeds may have been acquired independently in different localities, there is no greater difficulty in supposing that a simple suppression of the posterior pleurobranch may also have occurred more than once in the evolution of the family. In all the groups of animals composing the remarkable fauna of Tanganyika, there is reason to believe that many of the endemic genera and species have been differentiated within the limits of the lake itself; and until the Atyidæ with a reduced branchial formula are shown to have a much wider geographical distribution than is at present known, it seems impossible to believe in a direct affinity between the Tanganyikan Atyella and the West Indian Calmania.

It may be freely admitted that these phylogenetic speculations rest upon much less solid ground than do the conclusions drawn directly from experiment or based upon statistics; but unless we are to abandon all hope of rationalising the facts of systematic and geographical biology, some such hypotheses are, for the present, indispensable.

List of Papers referred to.

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